

# UNDERSTANDING BLACKBIRD SENSORY SYSTEMS AND HOW REPELLENT APPLICATIONS WORK

SCOTT J. WERNER, United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, 4101 LaPorte Avenue, Fort Collins, CO 80521-2154, USA

LARRY CLARK, United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, 4101 LaPorte Avenue, Fort Collins, CO 80521-2154, USA

**Abstract:** We reviewed the learning processes and sensory capabilities of birds, with a special emphasis on chemical repellents and wildlife damage management. Repellents include several methods and devices used to manipulate behavior of birds in attempt to reduce damage or nuisance. Effective applications of chemical repellents to reduce bird damages are dependant upon an adequate understanding of the sensory modalities and modes of animal learning that are affected by a repellent. Chemical repellents can elicit withdrawal from specific or combined sensory stimuli or by producing learned avoidance via association between adverse postingestive effects and specific sensory cues. The application of repellents that elicit responses other than avoidance may result in a continued cycle of destructive sampling behavior and iterative escape. Avoidance is characterized by the discontinued sampling or consumption of foods, and/or the discontinued occupancy of places, previously associated with an aversive stimulus. Thus, an organism exhibits avoidance by evading an aversive event (e.g., adverse postingestive effects) and its associated cues (e.g., taste, odor, visual cue). An understanding of how an animal senses and integrates such cues and aversive events is necessary for the development and application of effective repellents. Although the efficacy of chemical repellents has not been comprehensively evaluated, we review recent modeling efforts that have identified the chemical properties of existing and candidate repellents for future applications.

**Key words:** *Agelaius phoeniceus*, behavior, chemical repellent, learning, *Molothrus ater*, *Sturnus vulgaris*, wildlife damage management.

Blackbirds are among the most abundant avian species in North America (Blackwell and Dolbeer 2001), and they can cause significant loss to fruit and grain producers in many parts of the United States. Repellents are sometimes used to resolve conflicts that result from such economic losses, but few repellent products are commercially available. As a result, there is continuing interest in identifying new products to manage depredation (Clark 1998).

Repellents include a broad range of methods and devices used to manipulate behavior of birds in an attempt to reduce damage or nuisance. Important to the design and use of these methods and devices is an adequate understanding of the sensory modality mediating perception of the signal and the modes of animal learning as applied to contextually appropriate circumstances. In short, the success of a repellent is fundamentally tied to the axiom of using the proper tool for the proper job. When repellents “fail” it is because we, as wildlife managers, have failed to appropriately match signal, receiving system, message, and context. Reconciling these considerations is by no means a trivial process. As a first step in better preparing us for successful management, this paper is intended as a brief review of the components of the processes described. Toward this end, we review the processes of learning

and capabilities of the sensory systems of birds, with a special emphasis on chemical repellents.

## PRIMARY AND SECONDARY CHEMICAL REPELLENTS

Fundamental to the successful development and application of repellents, regardless of the sensory system involved, is a clarification of the types of behaviors the repellent might produce. In the context of wildlife damage management, chemical repellents are applied to alter the feeding habits and the location of depredating animals (Rogers 1974). Chemical repellents can act by eliciting (proximate) withdrawal from specific or combined sensory stimuli (e.g., odor, taste; Rogers 1974), or by producing learned (ultimate) avoidance via association between adverse postingestive effects and specific sensory cues (e.g., taste, odor; Rogers 1974).

The terms primary and secondary repellents have been used to characterize the mode of action of repellents (Clark 1997b). Primary repellents possess a quality (e.g., unpalatable taste, odor, irritation; Clark 1998) that evokes reflexive withdrawal or escape behavior in an animal. In contrast, secondary repellents evoke an adverse physiological effect (e.g., illness, pain), which

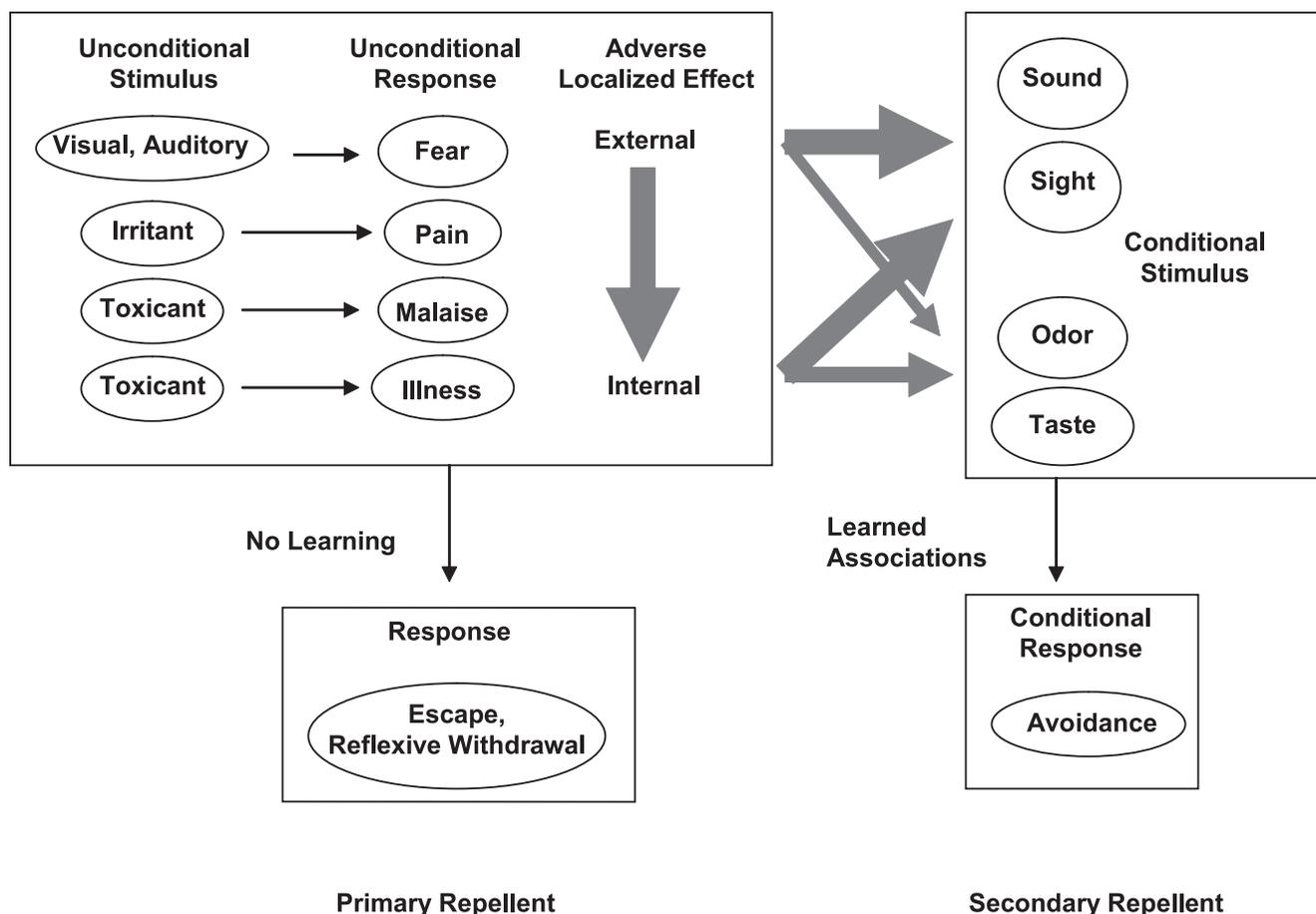
in turn is associated with a subsequently-avoided sensory stimulus (e.g., taste, odor, visual cue; Clark 1997b).

**PROCESSES IMPORTANT FOR REPELLENCY**

Repellents may give rise to escape or avoidance behavior (Fig. 1). It is important not to equate the two. An animal may reflexively withdraw from a stimulus or from the area where the stimulus was applied because the stimulus was painful or frightening. The escape behavior may even result in the animal leaving an area and other circumstances may diminish the likelihood of it returning. The manager may thus believe that he or she has effected a sound repellent strategy. However, in the case of neophobia, the animal's fear of the novel stimulus soon diminishes. In the case of reflexive withdrawal from a painful stimulus, the animal may not have learned target-oriented avoidance, and this might result in a continued cycle of destructive sampling

behavior and iterative escape. Avoidance is characterized by the discontinued sampling or consumption of foods, and the discontinued occupancy of places, previously associated with an aversive stimulus. Thus, an organism exhibits avoidance by evading an aversive event (e.g., adverse postingestive effects) and its associated cues (e.g., taste, odor, visual cue).

There are 4 critical features important to the functioning of secondary repellents and learned avoidance behavior (Fig. 1). The repellent (unconditional stimulus, US) elicits an unpleasant experience (unconditional response, UR) in the animal. The animal associates the UR with sensory cues (conditional stimuli, CS) paired in space and time to form the learned avoidance (conditional response, CR) (Pavlov 1906, Garcia et al. 1966). Garcia (1989) suggested that animals cognitively associate a CS (e.g., odor, sight of food) and US (taste) associated with food. Feedback (UR) associated with



**Fig. 1. Conceptual model for repellency.** Primary repellents are compounds that evoke reflexive withdrawal or escape behavior immediately after exposure. Secondary repellents are avoided because an animal associates an aversive experience (e.g., illness, pain) with a sensory stimulus. Birds can be trained to avoid otherwise innocuous stimuli (e.g., tastes [Schuler 1983], odors [Clark and Mason 1987], and visual cues [Brower 1969, Mason and Reidinginger 1983]) when these cues are paired with an illness-producing agent. Understanding the mechanism underlying the avoidance response and identifying the sensory system that contributes to that response are important for the development and application of effective chemical repellents. Arrow width represents relative likelihood of response-stimulus association among birds.

ingesting such foods (i.e., positive and negative post-ingestive consequences), and subsequent selection or avoidance (CR), emerge as involuntary (noncognitive) responses (Garcia 1989).

Pelchat et al. (1983) found that learned aversions were strongest if the US induced gastrointestinal illness rather than peripheral discomfort. Indeed, skin defenses are readily associated with contextual cues of place, and gut defenses are well associated with tastes (Garcia and Hankins 1977). Domjan (1998) suggested that the magnitude of the conditioned avoidance response is directly related to level of discomfort (UR intensity). We would expect that chemicals acting enterally have the best chance at being effective repellents that promote long-term learned avoidance, whereas chemicals acting externally or peripherally may be less effective repellents because the animal can limit its exposure to the US (Sayre and Clark 2001).

Although myriad UR-CS pairings exist, certain associations are more frequently paired in nature and thus more readily established (Milgram et al. 1977). For example, aversions based on flavor cues and gastrointestinal illness are readily made by mammals because they both are associated with eating (Revusky 1977). The neural convergence hypothesis suggests that visceral afferents interact with gustatory and olfactory afferents in the solitary nucleus of the brain stem to facilitate or inhibit food ingestion (Provenza 1995), thus a neurophysiological basis exists for aversive conditioning and food selection (Garcia 1989). Relative to mammals, birds have excellent color vision and can even detect and respond to ultraviolet wavelengths (see below). Birds have also been observed to form visual-illness associations (Mason and Reidinger 1983). Thus, the development and application of effective repellents (i.e., reliable CR) are contingent upon our understanding of how an animal will sense and integrate the adverse experience.

## UNDERSTANDING THE SENSES

The primary mediating sensory modalities targeted by repellent applications include the chemical senses, vision (sight), audition (hearing), and touch (e.g., polybutenes). If the chemical senses are treated as one, the likelihood that a chemical repellent will fail is high because it will be designed and delivered in a contextually inappropriate manner. The chemical senses of an animal are composed of olfactory (smell), gustatory (taste) and chemesthetic (irritation and pain) systems (Mason and Clark 2000). In terms of chemical signals, the integrated perception of all 3 chemosensory inputs is called flavor. Unlike hearing and sight, where the signals are distinctly different in nature, the chemical senses involve similar stimuli mediated through differ-

ent sensory systems which in turn provide the context of the message.

## Olfaction

Olfaction acts as a telereceptive system, capable of receiving airborne chemical stimuli in extreme dilution over relatively great distances. Olfactory receptors are located in the nasal conchae. Odors are typically received through the nares during respiration, and they then pass over the olfactory epithelium (Bang and Wenzel 1986). Except for the Kiwi (*Apteryx* spp.), birds do not sniff (Wenzel 1968). Therefore, obvious olfactory sampling behaviors are absent in birds. Nonetheless, olfaction is important to their evaluating palatability of food. Volatiles from food held in the mouth travel retronasally to the nasal conchae and to the olfactory receptors. Extensive research indicates that many species of birds have an adequate to excellent sense of smell (Wenzel 1973, Bang and Wenzel 1986, Waldvogel 1989, Roper 1999). Thus, the extent of olfactory development in birds is comparable to that found in mammals (Mason and Clark 2000).

The best known studies of avian olfaction involved pigeon (*Columba* spp.) homing behavior, food and burrow orientation by petrels (*Pterodroma* spp.), and food location by vultures (*Cathartes aura*, *Corygyps atratus*). These studies and others (Bingman and Benvenuti 1996, Roper 1999) have shown that olfaction is used by birds for the processes of orientation and food selection. Behavioral and physiological data have further illustrated the ecological significance of olfaction to passerines (Clark and Mason 1987, 1989; Clark and Smeraski 1990). A comparative evaluation of passerine olfaction revealed that insectivores are characterized by relatively poor olfaction, whereas birds that are primarily frugivorous, omnivorous, and granivorous have a relatively good sense of smell (Clark et al. 1993). For example, the detection threshold for a standard odorant ranged from 6.8 to 86.5 ppm for cedar waxwings (*Bombycilla cedrorum*; predominantly frugivores) and 73.4 to 317.8 ppm for insectivorous tree swallows (*Tachycineta bicolor*; Clark 1991). Despite the relatively poor development of olfactory anatomy among passerines, these birds possess an adequate sense of smell comparable to that of rats and rabbits (Clark et al. 1993).

Olfactory cues may serve as conditional stimuli to which learned aversions can be formed when paired in the presence of toxicants or irritants (Clark and Mason 1987). Rogers (1974) suggested that the most likely candidates for effective avian repellents will come from those chemicals that are capable of producing conditioned aversions (i.e., avoidance rather than escape) in the target species. Similarly, Provenza (1997) suggested

that deterrents based merely on offensive flavors or altered flavors associated with a familiar food are not likely to be effective in the absence of aversive, post-ingestive effects. For example, the novel odor associated with pyrazine is not repellent to red-winged blackbirds (*Agelaius phoeniceus*) in captivity. However, pyrazine paired with post-ingestive malaise effectively reduced rice consumption subsequent to a conditioned flavor aversion (Avery and Nelms 1990). In view of these observations, more detailed and extensive investigations regarding the role of novel and salient flavors in blackbird chemical repellent applications are needed.

### Gustation

Relative to olfaction, gustation requires a more intimate contact between the source of the chemical signal and the receptors. Gustatory receptors are located in taste buds throughout the oral cavity. For humans, the sensations of taste are restricted to assessment of sweetness, sourness, saltiness, bitterness, and savory (Kare and Brand 1986, Burgard and Kuznicki 1990). Not all species perceive all five taste qualities, but taste among bird species is generally limited to these qualities. Sensitivity among birds to “tastants” reflects species-specific ecologies and food habits and follows the same patterns seen in mammals (Rensch and Neunzing 1925, Engelmann 1934, Kare and Ficken 1963, Gentle 1975, Kare and Rogers 1976, Berkhoudt 1985).

Relative to other vertebrates, birds have few taste buds (Mason and Clark 2000). Unlike mammals, avian taste buds are not located in the papillae or the anterior tongue. Rather, the greatest concentration of taste receptors in birds is found on the posterior tongue and floor of the pharynx. Taste impulses in birds are carried only in the glossopharyngeal nerve (posterior third of tongue) and, unlike mammals, not at all in the facial nerve (Wenzel 1973). Rather, glossopharyngeal afferents in birds enter the medulla and join fibers from the facial and vagus nerves to form the fasciculus solitarius. Regardless of these anatomical considerations, Westbrook et al. (1980) observed “the primacy of taste in the formation of food aversions,” and the mediational role of taste in the formation of aversions to the exteroceptive attributes (e.g., color) of a food object.

### Irritation

Chemesthesis is the perception of chemically irritating or painful nociceptive stimuli (Mason and Clark 2000). Nociceptors are specialized neurons that provide animals with information about the noxiousness of chemical, mechanical, and thermal stimuli. Because nociceptors provide an animal with information about tissue damage, or the threat of damage, they arguably serve an adaptive function (Clark 1997b). Noxious chemical stimuli might give rise to different qualitative

perceptions, depending upon the nature of the activating stimulus. For example, animals possess a variety of neurochemicals that code for different qualities of noxiousness (Terenius 1987, Jessell and Kelly 1991).

Stabbing, throbbing, burning, and itching are human descriptions of perception mediated by nociceptors and activated by specific neurochemicals when tissue damage occurs. The cell damage results in the release of peptides (e.g., bradykinin, substance P [SP]), amines (e.g., serotonin, histamine), arachidonic acid derivatives (e.g., prostaglandins), and acetylcholine. The threshold for tolerance of nociceptive signals, mediated by the central nervous system, dictates the perception of whether or not a noxious stimulus is painful. An animal's willingness to tolerate pain is subject to its motivational state (Melzack 1973). Exogenous chemicals that are used as repellents are believed to mimic the qualities of these endogenous neurochemicals, thus providing an explanation for the repellency of irritants (Clark 1998).

The underlying physiological and biochemical processes mediating nociception appear to be similar for birds and mammals. Neurochemicals such as bradykinin, SP, serotonin, and acetylcholine evoke pain-related behaviors in chickens (*Gallus gallus*), rock doves (*Columba livia*), and guinea pigs (*Cavia* spp.) (Szolcsanyi et al. 1986, Gentle and Hill 1987, Gentle and Hunter 1993). Prostaglandins, which modulate the pain response in mammals, also do so in birds (Macari et al. 1993, Clark 1995). In European starlings (*Sturnus vulgaris*) as in mammals, the effects of prostaglandins can be abolished by prostaglandin biosynthesis inhibitors, i.e., aspirin-like analgesics (Clark 1995). Despite the similarities in neurotransmitter function there are differences in receptor function (M. L. Kirifides et al., unpublished data) and these differences are manifested in differences between birds and mammals in behavioral sensitivity to chemicals (Clark 1998). This explains why chemicals like capsaicin, mustard oil, and ammonia are irritating to mammals and not to birds (Mason and Clark 1995), and why chemicals such as anthranilates and acetophenones are repellent to birds and generally not to mammals.

Birds can detect volatiles, and they can be trained to avoid them (Michelsen 1959, Henton et al. 1966, Henton 1969). However, unconditioned avoidance occurs at high concentrations (> 10% vapor saturation, Tucker 1963, 1971; Silver and Maruniak 1980, Keverne et al. 1986, Stevens and Clark 1998) and requires stimulation of the ophthalmic branch of the trigeminal nerve (OBTN, Walker et al. 1979, 1986; Mason and Silver 1983). Starlings with the OBTN intact, but with the olfactory nerve (ON) transected, continue to avoid food treated with coniferyl benzoates, which are aromatic compounds with structural properties similar to the anthranilates (Jakubas et al. 1992). Conversely, when

the OBTN is cut and the ON is left intact, avoidance of coniferyl benzoates is lost.

The role of chemesthesis as the primary sensory modality for the repellency of anthranilates is also illustrated in a study by Mason et al. (1989). Starlings given bilateral ON transects required slightly higher concentrations of anthranilates before they rejected treated food, suggesting that olfaction has some minor contribution to the avoidance response. In a separate study, Clark (1996) found that in the absence of oral contact olfaction has no modulatory effect on consumption. Bilateral transection of the ON as well as OBTN results in a substantial increase in anthranilate concentrations required for rejection of treated food, indicating the importance of trigeminal mediation for the avoidance response, and the importance of the interaction between chemesthetic and olfactory systems when stimuli are presented orally (Mason et al. 1989). It is not surprising that the avoidance response was not completely eliminated. Mandibular and maxillary branches of the TN were left intact. These branches of the TN, and possibly the gustatory nerves, contributed to the remaining, substantially diminished, avoidance response. Given the above observations it is clear that trigeminal irritants exert their influence when applied orally, nasally, or ocularly. Thus, it is important to remember that oral delivery of repellents does not necessarily imply that receptors in the oral cavity of birds mediate the avoidance response (Clark 1997b). Similar cautionary arguments hold for nasal and ocular presentations of irritants.

## Vision

Avian vision facilitates navigation, recognition of conspecifics and mates, predator avoidance, and food selection. Light is detected via the optic nerve. Unlike the anatomy of the mammalian eye, the avian eye contains retinal pecten, oil droplets (within cones) for intraocular color filtration, and a nictitating membrane (or third eyelid; Coppinger 1967). The avian cornea is thinner than that of mammals and striated musculature enables partial voluntary control of the pupil (Willis and Wilkie 1999). The retina of birds is unique among vertebrates in that the cone population of most avian retinas is relatively high (Sillman 1973).

The spectral sensitivity of a bird's cones is dependent upon the product of oil-droplet transmittance and the absorbance of the visual pigment (Varela et al. 1993). European starlings have a low photopic (bright-light vision) threshold associated with green, and high thresholds associated with blue and red (Adler and Daland 1959). The color vision of pigeons is thought to be similar to an aphakic (lens-less) human, though pigeons are more sensitive to short wavelengths (violet and near ultraviolet light) than humans (Blough 1961).

Bowmaker (1977) suggested that wavelengths associated with visual pigments within cones of pigeons vary from 460 to 569 nm. The peak absorbance ( $\lambda_{\text{max}}$ ) for pigeons and brown-headed cowbirds (*Molothrus ater*) is 544 nm and 501 nm, respectively (Sillman 1969). More recent evidence suggests that birds can generally distinguish colors ranging from 350 nm (ultraviolet) to 750 nm (red; Bowmaker 1987). In contrast to humans (3 pigments), birds have been shown to process 4 or 5 visual pigments that are maximally sensitive to differing spectral regions (Bowmaker 1987). Such tetra- or pentachromatic color vision has pronounced implications for avian ecology and bird damage management.

While tastes are likely the most potent conditional stimuli in the process of mammalian food consumption (Garcia et al. 1977), Wilcoxon et al. (1971) discovered that food preference in bobwhite quail is affected by the color of food, and visual stimuli can actually overshadow salient tastes upon conditioning illness-induced aversions. Similarly, Mason and Reindinger (1983) found that food aversions could be reliably conditioned in red-winged blackbirds using toxic gavage (methiocarb and lithium chloride) paired with colored oats. Oats that were colored differently than the color paired with lithium chloride were preferred through 4 weeks of post-treatment testing. Thus, at least in granivorous birds, color might be the dominant cue during the food consumption process and visual stimuli may enhance the efficacy of chemical deterrents (Avery and Mason 1997, Nelms and Avery 1997). Intense light (Lustick 1973) and low-powered lasers (Blackwell et al. 2002) have also been used to disperse birds associated with agricultural depredation.

## Audition

Sounds provide birds with information regarding territorial defense, mate selection, navigation, and recognition of predators, conspecifics, and prey location (Gill 1990). The vestibulocochlear nerve enables hearing among animals. While birds are generally most sensitive to sound frequencies that range from 1 to 6 kHz, the lower and upper frequency limits of avian hearing generally range from 0.1 to 0.4 kHz and 3 to 21 kHz, respectively (Schwartzkopff 1955, 1973; Frings and Slocum 1958). Thus, the frequency range of good hearing is narrower in birds than in mammals (Schwartzkopff 1973, Gill 1990). The upper limit of hearing in the European starling is approximately 16 kHz (Frings and Cook 1964). In general, passerines hear high frequency sounds better than non-passerines, and non-passerines hear low frequency sounds relatively well (Dooling 1982). For example, homing pigeons can detect sounds in the 1 to 10 Hz range (i.e., infrasound) that are 50 decibels lower than those audible to humans (Kreithen and Quine 1979).

Auditory repellents include both sonic and ultrasonic devices (Mason and Clark 1997). Sonic repellents used to disperse birds include propane canons, electronic and mechanical noise systems, and pyrotechnics. Although the effectiveness of ultrasonic repellents has been suggested for roosting and loafing birds, these devices may have little utility since frequencies in excess of 20 kHz are inaudible to birds (Mason and Clark 1997). Langowski et al. (1969) evaluated the effectiveness of a pure tone and a distress cry for repelling European starlings in captivity. The starling distress cry (60 to 100 decibels,  $\leq$  95 sec duration) was more repellent than the pure tone, though differing frequencies of the pure tone (1.0 to 7.5 kHz) also interrupted feeding cycles. Thus, auditory stimuli might be used to effectively reduce blackbird impacts to agricultural production (Conover 1984).

### CHEMICAL STRUCTURE OF CANDIDATE REPELLENTS: FUTURE DIRECTIONS

There is no single compendium for the evaluation of chemical bird repellents. The most extensive evaluation was performed by Schafer et al. (1983), who screened the toxicological and repellent potential of over 1,000 compounds. While these tests were based upon a limited number of assays and relatively small sample sizes, they serve as a good foundation for repellent evaluation of a diverse array of chemicals. Any number of individual studies also have surveyed for bird repellent properties of natural products, including D-pulegone (Mason 1990, Wager-Page and Mason 1996), Cinnamamides (Crocker and Perry 1990, Crocker et al. 1993), and registered pesticides (Avery and Decker 1992, Dolbeer et al. 1994, Clark 1998). Clark (1997a) summarized the bird repellent effects of 117 carbocyclic compounds. Avery and Cummings (this volume) provide a review of currently registered products.

Clark (1998) provides a detailed review of the structure-activity relationships of aromatic chemical repellents. Factors that affect the delocalization of lone pairs of electrons around the aromatic structure contribute to modifying the repellent effect. Acidic substituents to the benzene ring generally detract from repellency, and this effect is amplified if the acidic function is contained within the electron withdrawing group. Electron donation to the benzene ring enhances repellency. Substituents that contribute to basicity of the molecule (e.g., amines, methoxy groups) contribute to potency. Heteroatoms that distort the plane of the aromatic structure tend to lessen repellency, whereas factors that strengthen planarity (e.g., H-bonds, covalent heterocycles) tend to increase repellency (Clark et al. 1991, Clark and Shah 1991, 1994; Mason et al. 1991, Shah et al. 1991, 1992; Clark and Aronov 1999).

This modeling approach can be reduced to the following observations: The strongest repellents are aromatic heterocycles containing nitrogens and simple acetophenone structures. Aromatic N-heterocycles are more uniformly repellent than are acetophenones. Compounds derived from S-heterocycles, anthranilates, aromatic alcohols, and aromatic aldehydes tend to be moderately good repellents. Birds that consume alcohols show signs of toxicosis; thus, these compounds are not strictly primary repellents. Anthranilates and aldehydes result in a high degree of variability for activity. Benzoic acids are not, as a class, good repellents. Amino acids are not repellent. Terpene compounds, which are by far the largest and most diverse set of natural plant products used in plant-insect chemical defense are largely unstudied for their avian repellent potential (L. Clark and M. Parks, unpublished data).

### CONCLUSION

Conflicts that sometimes emerge from human-wildlife interactions typically involve specific foods and places selected by wildlife. Chemical repellents can be used to alter the foraging behavior and/or spatial preference of wildlife associated with such conflicts. Primary repellents are compounds that evoke reflexive withdrawal or escape behavior immediately after exposure. Secondary repellents cause adverse physiological effects and subsequent avoidance of associated sensory cues. An understanding of how an animal senses and integrates such cues and aversive events is necessary for the development and application of effective repellents. Although the efficacy of chemical repellents has not been comprehensively evaluated, recent modeling efforts have identified the chemical properties of existing and candidate repellents for future applications.

### LITERATURE CITED

- ADLER, H. E., AND J. I. DALLAND. 1959. Spectral thresholds in the starling (*Sturnus vulgaris*). *Journal of Comparative and Physiological Psychology* 52: 438-445.
- AVERY, M. L., AND D. G. DECKER. 1992. Repellency of cinnamic acid esters to captive red-winged blackbirds. *Journal of Wildlife Management* 56: 800-805.
- AVERY, M. L., AND J. R. MASON. 1997. Feeding responses of red-winged blackbirds to multisensory repellents. *Crop Protection* 16:159-164.
- AVERY, M. L., AND C. O. NELMS. 1990. Food avoidance by red-winged blackbirds conditioned with a pyrazine odor. *Auk* 107:544-549.

- BANG, B., AND B. M. WENZEL. 1986. Nasal cavity and olfactory system. Pages 195-225 in A. S. King and J. McLellan, editors. Form and function in birds. Volume 3. Academic Press, London, United Kingdom.
- BERKHOUDT, H. 1985. Structure and function of avian taste receptors. Pages 463-495 in A. S. King and J. McLellan, editors. Form and function in birds. Volume 3. Academic Press, London, United Kingdom.
- BINGMAN, V. P., AND S. BENVENUTI. 1996. Olfaction and the homing ability of pigeons in the southeastern United States. *Journal of Experimental Zoology* 276:186-192.
- BLACKWELL, B. F., G. E. BERNHARDT, AND R. A. DOLBEER. 2002. Lasers as nonlethal avian repellents. *Journal of Wildlife Management* 66:250-258.
- BLACKWELL, B. F., AND R. A. DOLBEER. 2001. Decline of the red-winged blackbird population in Ohio correlated to changes in agriculture. *Journal of Wildlife Management* 65:661-667.
- BLOUGH, D. S. 1961. Experiments in animal psychophysics. *Scientific American* 205:113-122.
- BOWMAKER, J. K. 1977. The visual pigments, oil droplets, and spectral sensitivity of the pigeon. *Vision Research* 17:1129-1138.
- BOWMAKER, J. K. 1987. Avian color vision and the environment. *Proceedings of the International Ornithological Congress* 19:1284-1294.
- BROWER, L. P. 1969. Ecological chemistry. *Scientific American* 220:22-29.
- BURGARD, D. R., AND J. T. KUZNICKI. 1990. Chemometrics: chemical and sensory data. CRC Press, New York, USA.
- CLARK, L. 1991. Odor detection thresholds in tree swallows and cedar waxwings. *Auk* 108:177-180.
- CLARK, L. 1995. Modulation of avian responsiveness to chemical irritants: effects of prostaglandin E1 and analgesics. *Journal of Experimental Zoology* 271:432-440.
- CLARK, L. 1996. Trigeminal repellents do not promote conditioned odor avoidance in European Starlings. *Wilson Bulletin* 108:36-52.
- CLARK, L. 1997a. A review of the bird repellent effects of 117 carbocyclic compounds. Pages 343-352 in J. R. Mason, editor. Repellents in wildlife management. National Wildlife Research Center, Fort Collins, Colorado, USA.
- CLARK, L. 1997b. Physiological, ecological, and evolutionary bases for the avoidance of chemical irritants by birds. *Current Ornithology* 14:1-37.
- CLARK, L. 1998. Review of bird repellents. *Proceedings of the Vertebrate Pest Conference* 18:330-337.
- CLARK, L., AND E. V. ARONOV. 1999. Human food flavor additives as bird repellents: I. Conjugated aromatic compounds. *Pesticide Science* 55:903-908.
- CLARK, L., K. V. AVILOVA, AND N. J. BEAN. 1993. Odor thresholds in passerines. *Comparative Biochemistry and Physiology* 104A:305-312.
- CLARK, L., AND J. R. MASON. 1987. Olfactory discrimination of plant volatiles by the European starling. *Animal Behavior* 35:227-235.
- CLARK, L., AND J. R. MASON. 1989. Sensitivity of brown-headed cowbirds to volatiles. *Condor* 91:922-932.
- CLARK, L., J. R. MASON, AND P. S. SHAH. 1991. Chemical repellency in birds: relationship between chemical structure and avoidance response. *Journal of Experimental Zoology* 260:310-322.
- CLARK, L., AND P. S. SHAH. 1991. Nonlethal bird repellents: in search of a general model relating repellency and chemical structure. *Journal of Wildlife Management* 55:538-545.
- CLARK, L., AND P. S. SHAH. 1994. Tests and refinements of a general structure-activity model for avian repellents. *Journal of Chemical Ecology* 20:321-339.
- CLARK, L., AND C. A. SMERASKI. 1990. Seasonal shifts in odor acuity by starlings. *Journal of Experimental Zoology* 177:673-680.
- CONOVER, M. R. 1984. Comparative effectiveness of Avitrol, exploders, and hawk-kites in reducing blackbird damage to corn. *Journal of Wildlife Management* 48:109-116.
- COPPINGER, L. L. 1967. The role of the avian visual system in crop depredation, with special reference to the red-winged blackbird. Thesis, University of Massachusetts, Amherst, USA.
- CROCKER, D. R., AND S. M. PERRY. 1990. Plant chemistry and bird repellents. *Ibis* 132:300-308.
- CROCKER, D. R., S. M. PERRY, M. WILSON, J. D. BISHOP, AND C. D. SCANLON. 1993. Repellency of cinnamic acid derivatives to captive rock doves. *Journal of Wildlife Management* 57:113-122.
- DOLBEER, R. A., M. L. AVERY, AND M. E. TOBIN. 1994. Assessment of field hazards to birds from methiocarb applications to fruit crops. *Pesticide Science* 40:147-161.
- DOMJAN, M. 1998. The principles of learning and behavior. Fourth edition. Brooks/Cole, Pacific Grove, California, USA.
- DOOLING, R. J. 1982. Auditory perception in birds. Pages 95-130 in D. E. Kroodsma and E. H. Miller, editors. Acoustic communication in birds. Academic Press, New York, USA.
- ENGELMANN, C. 1934. Versuche über den Geschmackssinn von Taube, Ente und Huhn. *Zeitschrift für vergleichende Physiologie* 1934:626-645.

- FRINGS, H., AND B. COOK. 1964. The upper frequency limits of hearing in the European starling. *Condor* 66:56-60.
- FRINGS, H., AND B. SLOCUM. 1958. Hearing ranges for several species of birds. *Auk* 75:99-100.
- GARCIA, J. 1989. Food for Tolman: cognition and cathexis in concert. Pages 45-85 in T. Archer and L. Nilsson, editors. *Aversion, avoidance and anxiety*. Erlbaum, Hillsdale, New Jersey, USA.
- GARCIA, J., AND W. G. HANKINS. 1977. On the origin of food aversion paradigms. Pages 3-19 in L. Baker, M. Domjan, and M. Best, editors. *Learning mechanisms in food selection*. Baylor University Press, Waco, Texas, USA.
- GARCIA, J., W. G. HANKINS, AND J. D. COIL. 1977. Koalas, men, and other conditioned gastronomes. Pages 195-218 in N. W. Milgram, L. Krames, and T. M. Alloway, editors. *Food aversion learning*. Plenum Press, New York, USA.
- GARCIA, J., R. KOVNER, AND K. F. GREEN. 1966. Cue properties vs. palatability of flavors in avoidance learning. *Psychonomic Science* 20:313-314.
- GENTLE, M. J. 1975. Gustatory behaviour of the chicken and other birds. Pages 305-318 in P. Wright and P. G. Caryl, editors. *Neural and endocrine aspects of behavior in birds*. Elsevier, Amsterdam.
- GENTLE, M. J., AND F. L. HILL. 1987. Oral lesions in the chicken: behavioural responses following nociceptive stimulation. *Physiology and Behavior* 40:781-783.
- GENTLE, M. J., AND L. N. HUNTER. 1993. Neurogenic inflammation in the chicken (*Gallus gallus var domesticus*). *Comparative Biochemistry and Physiology* 105C:459-462.
- GILL, F. B. 1990. *Ornithology*. W. H. Freeman and Company, New York, USA.
- HENTON, W. W. 1969. Conditioned suppression to odorous stimuli in pigeons. *Journal of the Experimental Analysis of Behavior* 12:175-185.
- HENTON, W. W., J. C. SMITH, AND D. TUCKER. 1966. Odor discrimination in pigeons. *Science* 153:1138-1139.
- JAKUBAS, W. J., P. S. SHAH, J. R. MASON, AND D. M. NORMAN. 1992. Avian repellency of coniferyl and cinnamyl derivatives. *Ecological Applications* 2:147-156.
- JESSELL, T. M., AND D. D. KELLY. 1991. Pain and analgesia. Pages 385-399 in E. R. Kandel, J. H. Schwartz, and T. M. Jessell, editors. *Principles of neural science*. Elsevier, New York, USA.
- KARE, M. R., AND J. G. BRAND. 1986. Interaction of the chemical senses with nutrition. Academic Press, New York, USA.
- KARE, M. R., AND M. S. FICKEN. 1963. Comparative studies on the sense of taste. Pages 285-297 in Y. Zotterman, editor. *Olfaction and taste*. Pergamon Press, London, United Kingdom.
- KARE, M. R., AND J. G. ROGERS. 1976. Sense organs. Taste. Pages 29-52 in P. D. Sturkie, editor. *Avian physiology*. Springer-Verlag, Berlin, Germany.
- KEVERNE, E. B., C. L. MURPHY, W. L. SILVER, C. J. WYSOCKI, AND M. MEREDITH. 1986. Nonolfactory chemoreceptors of the nose: recent advances in understanding the vomeronasal and trigeminal systems. *Chemical Senses* 11:119-133.
- KREITHEN, M. L., AND D. B. QUINE. 1979. Infrasound detection by the homing pigeon: a behavioral audiogram. *Journal of Comparative Physiology* 129A:1-4.
- LANGOWSKI, D. J., H. M. WIGHT, AND J. N. JACOBSON. 1969. Responses of instrumentally conditioned starlings to aversive acoustic stimuli. *Journal of Wildlife Management* 33:669-677.
- LUSTICK, S. 1973. The effect of intense light on bird behavior and physiology. *Proceedings of the Bird Control Seminar* 6:171-186.
- MACARI, M., R. L. RURLAN, F. P. GREGORUT, E. R. SECATO, AND J. R. GUERREIRO. 1993. Effects of endotoxin, interleukin-1-beta and prostaglandin injections on fever response in broilers. *British Poultry Science* 34:1035-1042.
- MASON, J. R. 1990. Evaluation of D-pulegone as an avian repellent. *Journal of Wildlife Management* 54:130-135.
- MASON, J. R., M. A. ADAMS, AND L. CLARK. 1989. Anthranilate repellency to starlings: chemical correlates and sensory perception. *Journal of Wildlife Management* 53:55-64.
- MASON, J. R., M. L. AVERY, J. F. GLAHN, D. L. OTIS, R. E. MATTESON, AND C. O. NELMS. 1991. Evaluation of methyl anthranilate and starch-plated dimethyl anthranilate as bird repellent feed additives. *Journal of Wildlife Management* 55:182-187.
- MASON, J. R., AND L. CLARK. 1995. Capsaicin detection in trained European starlings: the importance of olfaction and trigeminal chemoreception. *Wilson Bulletin* 107:165-169.
- MASON, J. R., AND L. CLARK. 1997. Avian repellents: options, modes of action, and economic considerations. Pages 371-391 in J. R. Mason, editor. *Repellents in wildlife management*. National Wildlife Research Center, Fort Collins, Colorado, USA.
- MASON, J. R., AND L. CLARK. 2000. The chemical senses in birds. Pages 39-56 in G. A. Whittow, editor. *Sturkie's avian physiology*. Fifth edition. Academic Press, New York, USA.

- MASON, J. R., AND R. F. REIDINGER. 1983. Importance of color for methiocarb-induced food aversions in red-winged blackbirds. *Journal of Wildlife Management* 47:383-393.
- MASON, J. R., AND W. L. SILVER. 1983. Trigeminally mediated odor aversions in starlings. *Brain Research* 269:196-199.
- MELZACK, R. 1973. *The puzzle of pain*. Basic Books, New York, USA.
- MICHELSSEN, W. J. 1959. Procedure for studying olfactory discrimination in pigeons. *Science* 130:630-631.
- MILGRAM, N. W., L. KRAMES, AND T. M. ALLOWAY. 1977. *Food aversion learning*. Plenum Press, New York, USA.
- NELMS, C. O., AND M. L. AVERY. 1997. Reducing bird repellent application rates by the addition of sensory stimuli. *International Journal of Pest Management* 43:187-190.
- PAVLOV, I. P. 1906. *Conditioned reflex*. Oxford University Press, Oxford, United Kingdom.
- PELCHAT, M. L., H. J. GRILL, P. ROZIN, AND J. JACOBS. 1983. Quality of acquired responses to tastes by *Rattus norvegicus* depends on type of associated discomfort. *Journal of Comparative Psychology* 97:140-153.
- PROVENZA, F. D. 1995. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. *Journal of Range Management* 48:2-17.
- PROVENZA, F. D. 1997. Origins of food preference in herbivores. Pages 81-90 in J. R. Mason, editor. *Repellents in wildlife management*. National Wildlife Research Center, Fort Collins, Colorado, USA.
- RENSCH, B. AND R. NEUNZING. 1925. Experimentelle Untersuchungen über den Geschmackssinn der Vögel II. *Journal of Ornithology* 73:633-646.
- REVUSKY, S. 1977. Learning as a general process with an emphasis on data from feeding experiments. Pages 1-71 in N. W. Milgram, L. Krames, and T. M. Alloway, editors. *Food aversion learning*. Plenum Press, New York, USA.
- ROGERS, J. G., JR. 1974. Responses of caged red-winged blackbirds to two types of repellents. *Journal of Wildlife Management* 38:418-423.
- ROPER, T. J. 1999. Olfaction in birds. *Advances in the Study of Behavior* 28:247-332.
- SAYRE, R. W., AND L. CLARK. 2001. Effect of primary and secondary repellents on European starlings: an initial assessment. *Journal of Wildlife Management* 65:461-469.
- SCHAFFER, E. W., JR., W. A. BOWLES, JR., AND J. HURLBUT. 1983. The acute oral toxicity, repellency, and hazard potential of 998 chemicals to one or more species of wild and domestic birds. *Archives of Environmental Contamination and Toxicology* 12:355-382.
- SCHULER, W. 1983. Responses to sugars and their behavioural mechanisms in the starling (*Sturnus vulgaris* L.). *Behavioral Ecology and Sociobiology* 13:243-251.
- SCHWARTZKOPFF, J. 1955. On the hearing of birds. *Auk* 72:340-347.
- SCHWARTZKOPFF, J. 1973. Mechanoreception. Pages 417-477 in D. S. Farner, J. R. King, and K. C. Parkes, editors. *Avian biology*. Volume 3. Academic Press, New York, USA.
- SHAH, P. S., L. CLARK, AND J. R. MASON. 1991. Prediction of avian repellency from chemical structure: the aversiveness of vanillin, vanillyl alcohol, and veratryl alcohol. *Pesticide Biochemistry and Physiology* 40:169-175.
- SHAH, P. S., J. R. MASON, AND L. CLARK. 1992. Avian chemical repellency: a structure-activity approach and implications. Pages 291-296 in R. L. Doty and D. Muller-Schwarze, editors. *Chemical signals in vertebrates*. Plenum Press, New York, USA.
- SILLMAN, A. J. 1969. The visual pigments of several species of birds. *Vision Research* 9:1063-1077.
- SILLMAN, A. J. 1973. Avian vision. Pages 349-387 in D. S. Farner, J. R. King, and K. C. Parkes, editors. *Avian biology*. Volume 3. Academic Press, New York, USA.
- SILVER, W. L., AND J. A. MARUNIAK. 1980. Trigeminal chemoreception in the nasal and oral cavities. *Chemical Senses* 6:295-305.
- STEVENS, G., AND L. CLARK. 1998. Bird repellents: development of avian-specific tear gases for resolution of human-wildlife conflicts. *International Biodeterioration and Biodegradation* 42:153-160.
- SZOLCZANYI, J., H. SANN, AND F. K. PIERAU. 1986. Nociception in pigeons is not impaired by capsaicin. *Pain* 27:247-260.
- TERENIUS, L. 1987. Pain, chemical transmitter concepts. Pages 901-903 in G. Adelman, editor. *Encyclopedia of neuroscience*. Birkhauser, Boston, Massachusetts, USA.
- TUCKER, D. 1963. Olfactory, vomeronasal and trigeminal receptor responses to odorants. Pages 45-69 in Y. Zotterman, editor. *Olfaction and taste*. Pergamon Press, New York, USA.
- TUCKER, D. 1971. Nonolfactory responses from the nasal cavity: Jacobson's organ and the trigeminal system. Pages 151-181 in L. M. Beidler, editor. *Handbook of sensory physiology*. Volume 4. Chemical senses. Part 1. Olfaction. Springer-Verlag, Berlin, Germany.

- VARELA, F. J., A. G. PALACIOS, AND T. H. GOLDSMITH. 1993. Color vision of birds. Pages 77-98 *in* H. P. Zeigler and H. J. Bischof, editors. Vision, brain, and behavior of birds. MIT Press, Cambridge, Massachusetts, USA.
- WAGER-PAGE, S. A., AND J. R. MASON. 1996. Exposure to volatile D-pulegone alters feeding behavior in European starlings. *Journal of Wildlife Management* 60: 917-922.
- WALDVOGEL, J. A. 1989. Olfactory orientation by birds. Pages 369-379 *in* D. M. Power, editor. Current ornithology, Volume 6. Plenum Press, New York, USA.
- WALKER, J. C., D. TUCKER, AND J. C. SMITH. 1979. Odor sensitivity mediated by the trigeminal nerve in the pigeon. *Chemical Senses and Flavour* 1979: 107-116.
- WALKER, J. C., D. B. WALKER, C. R. TAMBIAH, AND K. S. GILMORE. 1986. Olfactory and nonolfactory odor detection in pigeons: elucidation by a cardiac acceleration paradigm. *Physiology and Behavior* 38: 575-580.
- WENZEL, B. M. 1968. The olfactory prowess of the kiwi. *Nature* 220: 1133-1134.
- WENZEL, B. M. 1973. Chemoreception. Pages 389-415 *in* D. S. Farner, J. R. King, and K. C. Parkes, editors. Avian biology. Volume 3. Academic Press, New York, USA.
- WESTBROOK, R. F., J. C. CLARKE, AND S. PROVOST. 1980. Long-delay learning in the pigeon: flavor, color, and flavor-mediated color aversions. *Behavioral and Neural Biology* 28: 398-407.
- WILCOXON, H. C., W. B. DRAGOIN, AND P. A. KRAL. 1971. Illness-induced aversions in rat and quail: relative salience of visual and gustatory cues. *Science* 171: 826-828.
- WILLIS, A. M., AND D. A. WILKIE. 1999. Avian ophthalmology. Part 1: Anatomy, examination, and diagnostic techniques. *Journal of Avian Medicine and Surgery* 13: 160-166.